On the Taxonomic Position of Ellabella Busck, with Descriptions of the Larva and Pupa of E. bayensis (Lepidoptera: Copromorphidae)

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Abstract. The final instar larva, pupa, and some biological observations of Ellabella bayensis Heppner are described. The larval host is Mahonia pinnata (Lagasca) Fedde (Berberidaceae). Larval and pupal characters indicate that the genus Ellabella Busck, which has been placed in four families in three superfamilies since 1925, is in Copromorphidae. Although some characters vary from other Copromorphidae, others, especially chaetotaxy, support the transfer of Ellabella to that family.

Introduction

Busck (1925) described the genus and species Ellabella editha from moths collected in British Columbia and Alberta. He placed the genus in Glyphipterigidae (auctorum) based upon similarities in wing venation to those of Lotisma Busck and Araeolepia Walsingham. This treatment was followed by McDunnough (1939) even though Fletcher (1929) placed Ellabella and Lotisma in Yponomeutidae and Araeolepia in Plutellidae. Clarke (1955) transferred Ellabella to Ethmiidae following Meyrick (1927), who considered the genus (as Probolacma Meyrick) and Lotisma to be near Ethmia Huebner. However, Powell (1973) determined that characters of Lotisma and Ellabella were not gelechioid and removed both genera from Ethmiidae. Heppner (1978) transferred Ellabella and Araeolepia to Plutellidae and Lotisma to Copromorphidae in order to maintain consistency among the Glyphipterigidae (sens. str.).

Except in the case of Lotisma, Heppner's decisions were made without knowledge of the early stages. In April, 1981, I collected several larvae of a then undescribed Ellabella species on coastal barberry, Mahonia pinnata (Lagasca) Fedde (Berberidaceae). Heppner (1984) described this species as E. bayensis and suggested that the genus is likely in Copromorphidae. Larval and pupal characters indicate that Ellabella should not be placed in Plutellidae, and that although some characters are inconsistent with known Copromorphidae, others substantiate its placement in Copromorphidae.

Collection and Rearing Notes

Larvae were collected during April 1981 (J. De Benedictis Lot No. 81105-A and 81111-D) and April 1982 (Lot No. 82099-B and 82106-F) in the county park on San Bruno Mountain, San Mateo County, California. Larvae fed upon *Mahonia pinnata* (Lagasca) Fedde, coastal barberry. Coastal barberry sometimes is used as an ornamental in urban areas but is widespread and presumably native on San Bruno Mountain.

Except for two larvae found feeding in flowers, all larvae fed on new foliage. Old foliage is hard, spiny, and apparently seldom, if ever, fed upon by Lepidoptera larvae.

All but two foliage-feeding *E. bayensis* larvae were found in tightly-rolled new leaves, and both exceptions were smaller larvae. One was between the folded halves of a small leaf; the other was beneath a pad of silk on the underside of a new leaf and appeared to have been parasitized. Rolled shelters are constructed from a single leaf or from two or more overlapping leaves. Edges of the feeding shelter are sealed with a heavy silk seam except for a small opening through which frass is ejected.

Larvae apparently eat only the portion of leaves within the shelter then gnaw their way out to construct a new shelter. In one instance, silk led from an abandoned shelter to a flower cluster, but neither signs of feeding nor the larva were found. However, flower feeding may be more frequent than the two of the more than 50 larvae collected suggest. The yellow and green larvae closely match the flower colors, so larvae are difficult to locate within the flower clusters. On the other hand, larval coloration is a striking contrast to the bright red new leaves of coastal barberry.

Two larvae and a pupa from the 1981 collection and all larvae collected in 1982 were preserved in 95% ethanol after distension by boiling in water. The remainder of the 1981 collections was reared on cut foliage in plastic bags. The collections were housed in a mobile trailer lab with the minimum temperature controlled at approximately 19°C, so developmental times likely were not normal. Bags were inspected almost daily to collect emerging adults and to evert as necessary to release excess moisture.

Beginning in May, fully grown larvae ceased feeding and began constructing cocoons from materials in the rearing bags. Occasionally, they concealed themselves in dry foliage, but most larvae used the underlying paper towels or folds of plastic as the outer surface of the cocoon. Most chewed a semicircle in the paper towel or plastic, folded it over, and tied it with silk to the flat surface. A few sealed the edges of existing folds in the paper towels or plastic bags.

Development could be observed through the translucent plastic. Most larvae remained as prepupae for five or six months, but a few pupated within a week or two after spinning cocoons. Four adults emerged between late June and early July 1981, one emerged in early October, and 25 others emerged between late December 1981 and early March 1982. Pupal cases

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remained within the cocoons at eclosion.

Description of Early Stages

Final instar larva (Figures 1-5). Head (Figures 3-5): Width 1.31 to 1.47 mm, amber with darker crescent surrounding stemmata 1-5; frontal triangle slightly broader than high, tapering toward apex, extending nearly ¾ to epicranial notch; stemmata 1-6 in nearly evenly spaced semicircle except 5 displaced toward mouth; submental setae on small tubercales on V-shaped pigmented patch (Figure 5).

Body: Robust; distended length 9.2 to 14.3 mm; dorsum olive, occasionally with two indistinct narrow yellow-green longitudinal stripes; lateral and ventral surfaces yellow to yellow-green; one or two pairs or irregularly shaped dark brown blotches per segment in a dorsolateral longitudinal line from the prothorax immediately ventrad of cervical shield to segment A9; a narrow white longitudinal stripe adjacent and ventrad of line of blotches; dorsum exclusive of cervical shield lightly peppered with dark brown from prothorax to A9; unpigmented primary setae only, usually borne individually on small, weakly differentiated, sometimes amber pinnacula; setae relatively short.

Thorax: Cervical shield light to medium amber; prothorax with bisetose prespiracular group (L-group); prothoracic L- and SV-groups borne paired on amber pinnacula; prothoracic spiracle approximately twice the diameter of abdominal spiracles.

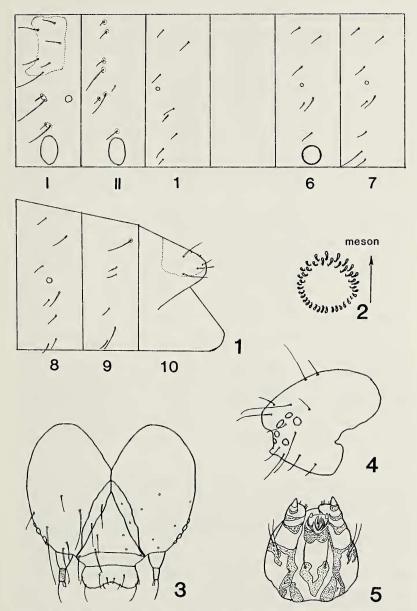
Abdomen: A1 with trisetose L-group, SV1 and V1 present, SD2 absent; spiracles placed somewhat anteriad near middle of segments, spiracle on A8 somewhat larger than others; A9 lacking D1; anal shield pale amber; prolegs on A3-6 and A10, short, cylindrical; crochets 35 to 44 in nearly uniordinal circle, mesal half of circle biserial, lateral half uniserial, lateral crochets often shorter than mesal (Figure 2).

Discussion: Based upon head capsule widths, 12 of 35 larvae were in the final instar. The remainder were in the penultimate and antepenultimate instars except one which was probably younger. Only the final instar is marked with the dark brown longitudinal lines of blotches and dorsal speckling. Earlier instars also differ in that head capsules and, sometimes, cervical shields are black.

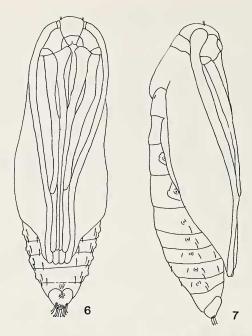
Pupa (Figures 6-7): Pale to deep amber; length 6.9 to 7.1 mm; fusiform; encased in silk-lined cocoon.

Head: Rounded anteriorly; two pair of setae on frons near antennal bases; antennae extending to wing tips near anterior margin of A9, not touching at ventral meson; eyes prominent, separated by relatively broad, somewhat trapezoidal labrum; triangular pilifiers laterad of labrum; labial palpi extending from base of labrum to A2; maxillae broad at base, laterad of labial palpi; haustellum extending nearly to wing tips along ventral meson; trangular maxillary palpi anteriad of tibiae of forelegs.

Thorax: Prothorax and mesothorax with a pair of short fragile setae near wing bases; forelegs laterad of maxillae, extending to A4, femora of forelegs partially visible between maxillae and tibiae of forelegs; mesolegs laterad of forelegs, extending nearly to wing tips; hindlegs concealed behind wings and haustellum except tarsi visible caudad of haustellum; wings long, extending to A9, not touching at ventral meson, hindwings visible as narrow strips dorsad of forewings; appendages caudad of A4 not touching abdomen.



Figs. 1-5. Larva. Fig. 1: Setal map. Roman numerals denote thoracic segments; arabic numbers denote abdominal segments. Fig. 2: Map of crochets on prolegs of A3-6. Fig. 3: Frontal view of head. Fig. 4: Lateral view of head. Fig. 5: Labium and maxillae.



Figs. 6 & 7. Pupa. Fig. 6: Ventral aspect. Fig. 7: Lateral aspect.

Abdomen: Spiracles protruding, those on A2 and 3 protrude from triangular elevated lobes; segments A5, 6, and 7, and 8-10, as a unit, moveable; abdominal setae short, fragile; one pair of dorsal setae on A7 and 8 only; A5-8 with three pairs of setae in double row ventrad of spiracles and single row approximately midway between spiracles and ventral meson; A4 with seta posterioventrad of each spiracle; A3-8 with a pair of setae in single row anteriodorsad of spiracles; cremaster of ten setae.

Discussion: In the lab, larvae roamed about actively just prior to pupation. The shelters constructed by captive larvae may simulate natural pupation sites not available in the rearing bags such as holes and crevices in twigs or soil or tunnels and gaps in leaf litter. I was unable to find pupae on the host plant in the field, which, together with the increased activity prior to pupation, suggests that pupation in nature occurs either off the host or in concealed niches on the host somewhere other than in the current year's foliage.

The inner surface of the cocoon is lightly lined with silk throughout. Silk is heavier around the seams and at the posterior end where the cremaster is attached.

The Taxonomic Position of Ellabella

Because adult characters indicate that *Ellabella* Busck is not in Ethmiidae nor in any other gelechioid family (Powell, 1973), larval and pupal characters of *E. bayensis* were compared only with the copromorphoid and yponomeutoid superfamilies and families using summaries

of characters (Common, 1970; Heppner, in review), descriptions of larvae (Werner, 1958; Yano, 1959; MacKay, 1972), and by examining preserved larvae from the Essig Museum of Entomology, University of California, Berkeley.

There is considerable disagreement between Common and Heppner on many character states. Some of the discrepancies can be explained by the transfer of some yponomeutoid families of Common to other superfamilies (Heppner, 1977), by differences in taxa included or examined within a family, and by information which became available subsequent to Common's summary. In some instances, however, I could not resolve the source of disagreement, but most may be due to the poor knowledge of the early stages of these taxa which has made family characteristics difficult to define.

Deciding the taxonomic position of *Ellabella* is further complicated by the absence of any exhaustive cladistic analysis of the higher categories of Lepidoptera either with or without consideration of the early stages. For example, Brock (1971) considered Copromorphoidea to be more ancestral than Gelechioidea, while Meyrick (1928) and Heppner (1977) both believe that Copromorphoidea is derived from the Gelechioidea. Thus, outgroup comparisons depend upon whose judgment is accepted. Despite these problems, there is justification for placing *Ellabella* in Copromorphidae, particularly if the transfer of *Lotisma* to Copromorphidae is correct (Heppner, 1978).

Ellabella bayensis exhibits most of the larval and pupal character states common to the Copromorphoidea (sensu Heppner, 1977). The larva has a bisetose prothoracic prespiracular group. With few exceptions, this character state occurs only in the Copromorphoidea and Pyraloidea among the Microlepidoptera. Exceptions include Scardia (Tineidae) (Hinton, 1956), Orthotaelia (Plutellidae) (Werner, 1958), Rhabdocosma (Plutellidae) (Heppner, in review), and Ocnerostoma (Yponomeutidae) (Werner, 1958).

Although there are pairs of fragile setae on A7 and 8, the pupa of *E. bayensis* lacks true dorsal abdominal spines. Its pupal shell is not protruded upon adult eclosion. Common (1970) asserts that mobile, well-spined pupae are primitive. Among the Microlepidoptera, non-protruded pupae occur throughout the Gelechioidea and Copromorphoidea and in most of the Yponomeutoidea.

These character states indicate that *Ellabella* is in the Copromorphoidea. With the exception of *Scardia*, the more ancestral Tineoidea and the probably more ancestral Gelechioidea have trisetose prothoracic L-groups. The bisetose state of the Copromorphoidea likely is derived by reduction.

The absence of true dorsal spination and the non-protrusion of the pupa at eclosion are more derived than the Tineoidea, but less derived than the J. Res. Lepid.

Gelechioidea whose pupae lack spines, have reduced setation and some mobility of abdominal segments, and are not protruded. In general, the pupa of *Ellabella* more consistently fits the concept of some Yponomeutoidea and Copromorphoidea in that pilifers, labial and maxillary palpi, and prothoracic femora are visible.

Few copromorphoid pupae have been described. However, Commatarcha palaeosoma Meyrick (Carposinidae) also has some dorsal setae and similar orientations of facial features and thoracic appendages (Yano, 1959). I compared the pupa of E. bayensis with that of Lotisma trigonana Walsingham, the only other Nearctic copromorphid genus. Lotisma and Ellabella pupae exhibit the same facial features and thoracic appendages in approximately the same locations. Lotisma pupae have some very frail dorsal abdominal setae and the same abdominal segments as E. bayensis are moveable. Unlike Ellabella, whose pupae are ensheathed in paper towels, plastic, or dried foliage, captive Lotisma larvae spin fluffy silken cocoons between overlapping leaves or in similar narrow spaces.

E. bayensis differs from other Copromorphoidea in larval feeding mode. Most known copromorphoid larvae bore or tunnel stems, roots, fruits, or flowers. However, Lotisma trigonana larvae often are external feeders of flowers or fruit, at least in later instars, so endophagy is not a constant feature of the Copromorphidae. At least occasionally, E. bayensis also feeds upon flowers, and the presence of one of the smallest larvae in a young leaf suggests that early instars mine leaf buds. Even if this character is not consistent with other copromorphoid larvae, the other shared derived characters of E. bayensis and the Copromorphoidea substantiate its superfamily placement.

Ellabella seems not to be a bisetose plutellid genus despite having some characteristics of that family. As with some plutellid larvae (e.g. Eucalantica polita Walsingham), the circle of crochets on prolegs of E. bayensis is biserial in part (Figure 2). This arrangement could be derived from the ancestral state, a single circle of crochets (Common, 1975), by offsetting some crochets in the circle. By contrast, the mesal penellipse of Lotisma trigonana presumably follows a different line of derivation in which a portion of the circle of crochets is lost.

E. bayensis and some plutellids (e.g. Homadaula) have protruding pupal spiracles. This may represent a derived state, but it occurs inconsistently among families including Epermeniidae and Glyphipterigidae in the Copromorphoidea so may be significant only at the generic level. However, L. trigonana also has protruding spiracles with those on A2 and 3 on triangular lobes as on E. bayensis.

Because the character states that *Ellabella* shares with some plutellids are not constant among the Plutellidae and because *Ellabella* possesses the derived character states common to most Copromorphoidea (*sensu* Heppner, 1977), the genus should not be placed in the Plutellidae.

Family characters also support the placement of *Ellabella* in Copromorphidae. D1 is absent on segment A9, and positions of most setae are very similar to those of *Lotisma trigonana* (see MacKay, 1972). *Ellabella* differs in having one rather than two pairs of subventral setae on A1, 2, and 7-9, and the spiracle on A8 is not on a tubercale as on *L. trigonana*. The submental setae of *E. bayensis* are located more caudad than those on *L. trigonana*, and the paired flaplike protrusions from the submentum of *Lotisma* are lacking. MacKay (1972) suggested that these submental characters may define the family, but the copromorphid genus *Isonomeutis*, for example, like *Ellabella*, has tuberculate submental setae and lacks protrusions (Heppner, in review). The submental setae of *Ellabella* are borne on a pigmented V-shaped patch which may represent another manner in which these setae are modified among the Copromorphidae.

The other copromorphoid families are inappropriate. *Ellabella* lacks the following characters of Glyphipterigidae, the only other copromorphoid family in which it has been placed: vestigial abdominal prolegs, spiracles on protuberances, and a large anal plate with stout setae. Moreover, D1 is always present on segment A9 in all copromorphoid families other than Copromorphidae in which this character varies.

Although Ellabella does not exactly fit the superfamily and family characters of Copromorphidae, this does not exclude it from the family. The taxa within a higher category define the characters of the higher category. Thus, in a poorly surveyed family such as Copromorphidae, the addition or exclusion of any genus may alter the presumed character states of the family considerably. Moreover, the notion that a suite of invariable characters defines the higher category presupposes that no evolutionary intermediacy exists. Ellabella may represent an intermediate genus, but its similarities to Lotisma and derived character states shared with the Copromorphoidea add validity to its assignment to Copromorphidae.

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